Forest Systems
24(3), eR01, 11 pages (2015)
eISSN: 2171-9845
http://dx.doi.org/10.5424/fs/2015243-07465
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA)

REVIEW ARTICLE

OPEN ACCESS

Response of European yews to climate change: a review

Peter A. Thomas[1]* and Xavier Garcia-Martí[2]

[1] *School of Life Sciences, Keele University, Staffordshire, UK.* [2] *Bioma Forestal, Etxauri, Navarra, Spain*

Abstract

Aim of study: Being the longest-lived of all European trees, capable of living significantly over 2,000 years, yew is highly likely to be negatively affected by climate change; this paper explores the changes in distribution and abundance.

Main results: Yew is unlikely to migrate north due to its slow rate of invasion, its disjunct soil needs and an inability to cope with the expected rate of climate change. It will, however, retreat from the southern end of its range in Spain due to increased evapotranspiration allied to reduced rainfall. In the south, increased drought will be exacerbated by extreme drought and increased fire frequency. In drier areas at the northern edge of its range, yew will decline where growing on well-drained limestone outcrops with little shelter from the sun (increased evaporation) and reduced water availability due to limited root spread. On wetter northern sites, yew should find better climatic conditions but will be slow to invade new areas due to poorer reproduction affected by reduced pollen production, population fragmentation and limited seed movement. Overall, without our intervention, yew will survive by inertia in the short-term but eventual become extinct in most areas. Of equal concern will be the loss of old veteran individuals and associated biodiversity.

Research highlights: There is an urgent need for interventionist management for both old and young trees, relieving the stress on old veteran trees, and planting and maintaining seedlings through vulnerable young age. A list of management priorities is given.

Keywords: Yew; *Taxus baccata*; temperature; precipitation; seedlings; bioclimate envelope; species range.

Citation: Thomas, P.A., Garcia-Martí, X. (2015). Response of European yews to climate change: a review. Forest Systems, Volume 24, Issue 3, eR01, 11 pages. http://dx.doi.org/10.5424/fs/2015243-07465.

Received: 30 Jan 2015. **Accepted:** 11 Sep 2015

Funding: The autor(s) received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist.

Correspondence should be addressed to Peter A. Thomas: p.a.thomas@keele.ac.uk

Climate Change in Europe

It is considered highly probable that the climate in Europe will indeed change over the next century, magnifying the current regional differences. Annual temperatures over Europe are due to increase with the greatest warming in southern Europe (Spain, Italy, Greece) and northeast Europe (Finland, western Russia) increasing by 4 °C by 2071-2100 (IPCC, 2013), with the least warming (<2 °C) along the Atlantic coastline. These differences will be particularly apparent in the south during the summer with southern Europe warming at a rate of between 0.2 and 0.6 °C per decade and northern Europe warming between 0.08 and 0.3 °C per decade. Annual precipitation is also likely to show a marked gradient with latitude with southern Europe becoming 15-20% drier (at a rate of 5% per decade) and Scandinavia and western Russia becoming 10-20% wetter (IPCC, 2013). This increasing latitudinal disparity in precipitation will also be more pronounced in summer, with the south being much drier and the north much wetter. Thus, in southern Europe, climate change is projected to worsen conditions for plants (high temperatures and drought), with an increase in wildfires, in a region already vulnerable to climate variability. The north and west will be less affected by long-term drought, and may instead suffer from increased periodic waterlogging or flooding, but high temperatures and episodes of water shortage by high evapotranspiration will be a problem.

Across Europe, these changes are likely to lead to extensive species loss (Allen *et al*., 2009), in some areas up to 60% loss of individuals (IPCC, 2013). Despite trees being robust to short-term weather changes there is also likely to be a long-term decline in some tree species (particularly northern spruces and pines) and an expansion of Mediterranean species, and a lowering in tree density (Hanewinkel *et al*., 2013). They suggest that the loss to forestry from these changes by 2100 will cost Europe >€190 billion.

Yew: a Tree under Threat

It has been recognised that yew (*Taxus baccata*) is a relic of a moderate Tertiary climate (Thomas & Polwart, 2003) and as a result of this ancestry modern trees grow best in the high humidity of mild oceanic climates, as do most other *Taxus* species (Figure 1). Thus, *Taxus baccata* forms dense, pure woodlands in the middle of its range across Central Europe into the British Isles, thinning out to small clumps and individual trees in moist niches at the extremities of its range, becoming a montane tree in the south and using the overstorey of other trees and north-facing slopes to provide oceanic-like conditions around each individual. It is also recognised that yew is undoubtedly the longest-lived of all European trees, readily reaching a maximum age of over 2,000 years and possibly even 5,000 years old (Thomas & Polwart, 2003).

Yew is under threat. It has become locally extinct or reduced to individual trees or small populations over the past 4,000 years in many parts of Europe and the former Soviet Union (Thomas & Polwart, 2003; Kassioumis *et al*., 2004) and this decline is continuing. This has led to many concerns over its long-term future (Dhar *et al*., 2006; Iszkuło *et al*., 2009; Linares, 2013; Devaney *et al*., 2014) and yew is now legally protected in a number of European countries (Hageneder, 2007) and has priority status under the EU Habitats Directive (European Commission, 2007). This decline is likely attributable to a wide range of reasons, undoubtedly partly due to climate change so far, but also due to excessive felling and other human disturbance.

However, the story of decline is not clear-cut since some populations have been seen to expand where conditions are suitable (Seidling, 1999) or management has been favourable (Svenning & Magård, 1999). In Norway, regeneration seems to be healthy (13,000+ 1-year old seedlings ha^{-1} – Dhar *et al*., 2006). Indeed, in the British Isles, Preston *et al*. (2002) show a slight expansion in yew distribution in the British Isles between 1930-69 and 1987-99 (although this may in part

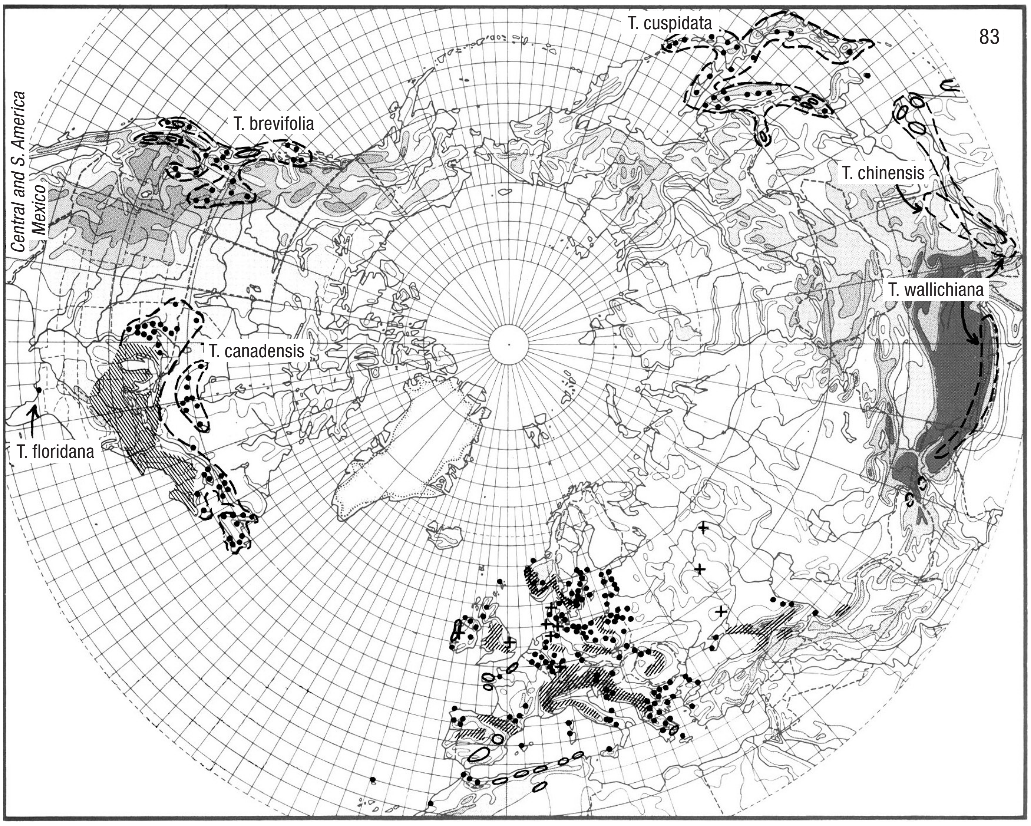

Figure 1. The circumpolar distribution of *Taxus baccata* and other *Taxus* species from Hultén & Fries (1986) showing that *Taxus* is a widespread genus, and many of the problems met by *Taxus baccata* in Europe are also being faced by other species globally; + indicates interglacial records; ● indicates isolated occurrences; hatched areas indicate regions of common or fairly common occurrence. Broken lines outline the distribution of *Taxus* species other than *T. baccata*. Reprinted with permission.

be due to changing from recording trees that were felt to be native to recording all trees whether native or introduced). Even in the southermost areas of Europe, an increase in some yew populations has been detected where conditions are currently climatically suitable, (annual rainfall >800 mm and mean evapotranspiration ≤700 mm y^{-1}) in both Atlantic and sub-Mediterranean biogeographic regions (Carvalho *et al*., 1999; Cortes *et al.*, 2000; Kassioumis *et al*., 2004; Fernandez-Manso *et al*., 2011; Serra & Garcia-Martí, 2011). In these cases, expansion occurred more than a decade ago before the abandonment of rural land and the consequent reduction in livestock pressure.

In summary, yew is a tree that has long been under threat in Europe despite some localised increase, and it is likely that climate change will be an increasing threat. Since it needs a fairly oceanic climate, and with individuals likely to meet a considerable change in climate over their long life, yew is highly likely to be negatively affected by changes in climate. Having said this, can we predict how yew will be affected across its wide European range?

How will Climate Change affect the Geographical Range of Yew?

It is expected that plant species in Europe will continue to move north as their preferred climatic conditions shift. On a world scale, Loarie *et al*. (2009) calculated that temperature bands are due to move north at an anticipated rate of 0.42 km y^{-1}. Plants are also moving up mountains for the same reason (Peñuelas *et al*., 2007). But it is not straightforward to predict how far trees will move northwards in the future.

It has so far proved difficult to match the current distribution of yew to specific climate parameters (the 'bioclimate envelope' – Pearson *et al*., 2002; Pearson & Dawson, 2003) due to the number of other factors affecting where the trees are found, particularly human exploitation and specific soil needs. An idea of the *potential* range of trees based on bioclimate envelopes has been produced by Sykes *et al*. (1996); this is bigger than the actual range due to the other factors such as suitable soils, topography and human interference. Svenning & Skov (2004) take this further and calculate the realised/potential (R/P) range using similar methods. Across all European tree species the mean R/P = 38% (±30% SD). For many dominant species, this ratio is higher (e.g. beech *Fagus sylvatica* 74%; oaks *Quercus robur/petraea* 91/84%) showing that they tend to fill the majority of their potential range. However for yew, R/P was calculated as 51%, indicating that it fills just over half of its potential range. This is obviously partly due to the fairly narrow soil requirements of yew, restricting where it grows even within a suitable climate. But even on wetter northern sites, where yew should find better optimum climatic conditions and would be less restricted to calcareous soils, it is absent.

This raises the question of whether the northwards shift in species range, by expansion in the north and contraction in the south, will actually happen in yew. Svenning & Skov 2004 build on this by suggesting that yew has been limited by poor dispersal ability from postglacial times onwards, so it is still slowly moving into suitable areas. Since yew has yet to catch up with 10,000 years of postglacial climate change, it is unlikely to respond with any speed to the current rapid rate of climate change. This may be compounded in the west of its range since here it is largely restricted to calcareous soils. These have a very patchy distribution and become a series of stepping stones with sufficiently large gaps between to prevent the spread of yew by seed. Further east and north, yew will grow on almost any soil (Elwes & Henry, 1906) but is still favoured by calcareous soil (Voliotis, 1986), so while this stepping stone affect may not prevent colonisation of new areas outside of western areas it is likely to have a weakening effect on new seedling establishment on sub-optimum soil.

Another facet controlling northerly migration is the need for the migrating species to be able to compete with the resident species. On calcareous soils, yew is a very strong competitor for light and water, resulting in few other trees, shrubs or herbaceous species surviving beneath the yews (Rodwell, 1991). However, on less favourable soils, yew faces competition from shade-tolerant trees such as *Fagus sylvatica* (Thomas & Polwart, 2003) which will further impede migration.

Many trees species are likely to show only limited tracking of fast climatic changes since conditions are generally happening too quickly to allow them to cope. For example, Zhu *et al*. (2012) working in eastern N. America suggest that as climate warms, seedlings should precede adult trees in the north (as the range expands) and the other way round in the south as range contracts due to loss of competitive advantage it had under cooler conditions. Despite the rate of change in temperature across the region being mostly slower than the global 0.42 km y^{-1} predicted by Loarie *et al*. (2009), Zhu *et al*. (2012) found that for many species this northerly expansion is not happening. For the 92 species they looked at, the average range contraction in the south was 29 km, much as expected. However, they also found a range *contraction* at the north end of 42 km. It appears that since seedlings are more sensitive to variations in temperature (as Grubb and

Harper both noted back in 1977), the climate is already too inhospitable at the north end of a tree's range to allow seedling establishment. Thus, it seems likely that many trees will have problems moving north, and yew will be particularly challenged since it is additionally burdened by its slow dispersal abilities and its edaphic needs.

This makes the prediction of the future distribution more difficult but it seems probable that yew will not migrate northwards at the rate suggested by suitable climatic envelopes, and indeed the northern range may even contract southwards as adult trees die.

In defiance of expectations it is likely that yew will not contract northwards away from the very southern end of its current. The southernmost remnant yew woods in Algeria (Riff and Telllian Atlas) and Morocco (Riff and Mid Atlas mountains) are located in humid and subhumid environments (Charco, 2007; Hamidouche *et al.*, 2014) where the rainfall currently exceeds 1,200 mm y^{-1}. This is more than the ecological requirement of yew, buffering individuals against climate change, particularly the vulnerable seedlings (Hamidouche *et al.*, 2014). Moreover, there is room for these populations to spread altitudinally at a local level if they can move fast enough. Further north, however, relict populations in the south-east of the Iberian Peninsula are in a much more vulnerable, marginal situation, already at the potential limit of their climatic tolerance. Current rainfall is already <600 mm y^{-1} in some places, and these populations are likely to go extinct. Contraction at the southern end of the range is thus likely to create disjunct populations.

What will happen to yew within its current range?

Taxus baccata is undoubtedly the most shade-tolerant tree in Europe (Thomas & Polwart, 2003), growing in <1% sunlight, although it survives and grows better with less shade outside of its own canopy. Seed production and subsequent seedling growth is also better under lighter shade (<5% sunlight) although yew seedlings will survive <2% full sunlight (Dhar *et al.*, 2007; Ruprecht *et al.*, 2010; Iszkuło, 2010; Linares, 2013). This should help yew to find suitable microclimates beneath the canopy of other trees. Yew is also very tolerant of high temperature, with an LT_{50} at 51 °C of 30 minutes (Lange, 1961). Similarly, the optimum temperature range for photosynthesis (14-25 °C) is the highest of any gymnosperm, with a summer maximum of 38-41 °C (Pisek *et al.*, 1969). It is therefore extremely unlikely that predicted higher temperatures by themselves will have a detrimental effect on yew. Yew is sensitive to prolonged and severe frost (Brzeziecki & Kienast, 1994), particularly in the spring. However, it is tolerant of low temperatures while winter hardened; needles in southern Sweden have been shown to survive −33 °C to −35 °C (Till, 1956). In terms of precipitation, *Taxus baccata* performs best under high humidity and rainfall; in England 80% of yew woods occur where maximum rainfall is >1000 mm y^{-1} (Tittensor, 1980) although at the southern end of its range it survives in small populations in as little as 569 mm y^{-1} (Mount Stratoniko, Greece), 564 mm y^{-1} (Chera Natural Park, Spain) and 518 mm y^{-1} (Pedro Andres, Spain) (Katsavou & Ganatsas, 2012; AEMET, 2014) but only where protected from excessive evapotranspiration by topography or a dense overstorey. Yew is tolerant of temporary waterlogging as can be caused by extreme weather events. Rather paradoxically yew is also tolerant of drought; Brzeziecki & Kienast (1994) ranked *T. baccata* as 2 in a 1–5 scale where 1 is very tolerant of drought.

The extra carbon dioxide fuelling climate change may itself increase growth of *T. baccata* but is likely to do so only under heavy shade (<1% sunlight) and possibly less than in its competitors such as *Fagus sylvatica* (Hättenschwiler & Körner, 2000; Hättenschwiler, 2001). Using this information, we can make some predictions as to what will happen to yew in different parts of its range.

1. Mid-range

In the main bulk of its range, overall temperature and precipitation changes over the next century by themselves should have little effect on regeneration and production of new trees, and may indeed improve regeneration. Moreover, unlike north of its current range, yew may possibly readily invade new areas (Tittensor, 1980), dependent upon the availability of spiny nurse plants such as juniper *Juniperus communis* to act as a perch for birds to drop yew seeds and to protect young seedlings from grazing (Williamson, 1978; García & Obeso, 2003). But climate change may affect the long-term survival of established individuals. With temperature bands due to move north by an average of 0.42 km y^{-1} (Loarie *et al.*, 2009) this means that over the life of a 2,000-3,000 year old tree that suitable conditions will have moved 850-1,270 km to the north. Given that the current north/south distribution of yew is around 3,000 km (Thomas & Polwart 2003) and that the speed of climatic shift is likely to increase, it is highly probable that old veteran individuals will progressively die over the next few centuries, thus removing one of the very distinctive features of the central European landscape.

2. Northern range

Towards the northern end of its current range, yew faces a number of problems, particularly as seedlings, including low temperatures, deep canopy shade, herbivory, and physiological drought in shoulder seasons when it is physiologically active and loosing water above-ground but the roots are too cold to function, and the seedlings faces effective drought (Sanz *et al*., 2009; Iszkuło, 2010; Linares, 2013). Indeed, Linares (2013) suggests that yew regeneration is already significantly lower above *c.* 55º latitude than further south although in reality this appears to be very variable with some populations showing significant regeneration. So, a warming climate with wetter summers, aided by less-dense woodland (brought about by a general disruption to plant communities in the face of species changes), should benefit seedlings and lead to an expansion in yew numbers within its current range providing that summer drought is not too intense. Certainly for yews growing on well-drained limestone outcrops where there is little shelter from the sun (and thus increased evaporation) and reduced water availability due to limited root spread, summer drought may indeed be limiting (Thomas & Polwart, 2003). Thus, the final picture is likely to be population growth on semi-shaded, damp sites and population contraction on more exposed sites.

3. Southern range

At the southern end of its range, yew populations are also likely to decrease due to increased temperatures acting mainly through increasing evapotranspiration, reinforcing the reduced water availability due to decreased summer precipitation creating drought conditions (Sanz *et al*., 2009; Mendoza *et al*., 2009b). As above, this is most likely to operate at the level of reduced numbers of seedlings. Certainly, yew seedlings are already scarce at the southern edge of its range compared to competitors such as hawthorn *Crataegus monogyna* and holly *Ilex aquifolium* (Mendoza *et al*., 2009a; Martínez *et al*., 2013). Fewer seedlings will leave an increasingly old set of individuals. Yew relies on extreme longevity and extreme shade tolerance to survive (Watt, 1926), so the remnant populations will likely survive for many years but individual trees will progressively reach an irreversible tipping point (Camarero *et al*., 2015) and so in turn will also succumb to the increasingly harsher climate.

Yew populations in S Spain (Figure 2a) are particularly threatened by water stress (Cortes *et al*., 2000; Costa, 2007; Garcia *et al*., 2000). As such, these populations can be monitored as key indicators of yew decline and their associated biodiversity in the south.

The gradual disappearance of yew in southern regions will not be determined directly by the steadily increasing physiological stress of low water levels but for a succession of associated disturbances including drought and recurring fires, particularly in the Mediterranean ecosystems of SE Spain (Piñol *et al*., 1998). For example, in 2013-14 a severe drought in relict yew woods in Valencia province resulted in <200 mm y^{-1}, representing <25% of normal annual rainfall (AEMET, 2014; Figure 2b). Low rainfall events such as these are clearly causing extensive mortality in the short term, which is likely to carry on even if normal rainfall levels are restored. For example after a drought in 1994, Mediterranean sclerophyllous tree species (that are more tolerant of drought than yew) were negatively affected physiologically for >3 years (Peñuelas *et al*., 2000).

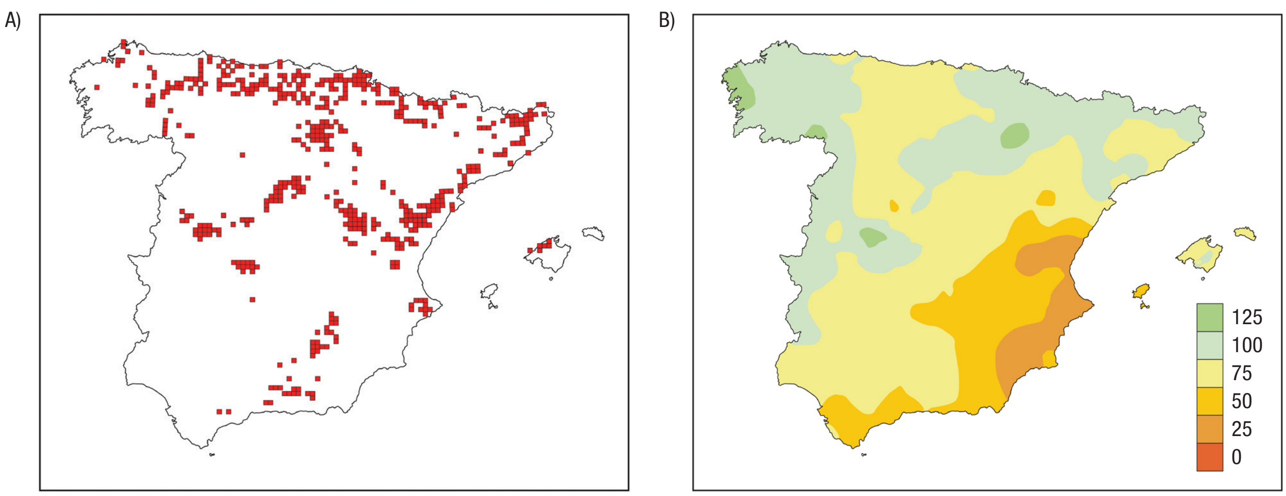

Figure 2. A) Distribution of yew population in Spain (modified Serra & Garcia-Martí, 2011), B) Percent of precipitation (normal to 1971-2000) falling in Spain in the year ending 30 September 2014 (data from AEMET, 2014).

Drought conditions also increase the frequency and intensity of wildfires. Certainly in the eastern Iberian peninsula, the number of fires per year has increased through the last two centuries (Pausas, 2004) leading to a degradation of relict yew woods and limiting potential regeneration in new sites as well due to their exposure. In Valencia province, the total number of individual yew trees has been reduced by 35% since the demographic records of Alcober *et al*. (1988) and another unpublished set of data, largely attributable to fires.

The associated effects of this drought and fire disturbance goes beyond just population decline of the yews, and includes: the subsequent loss of connectivity within and between populations; the negative effects of fragmentation and/or the reduction in habitat patch size; and a decrease in habitat quality by an increase in pioneer species which create habitat impermeable to the passage of yew (e.g. Saura *et al*., 2014). All of these factors make it more difficult for natural habitat restoration to occur and increases the probability of local extinction as part of the small population paradigm (Caughley, 1994). It is clear that the effects of climatic restrictions on the marginal southern populations of yew have been going on for some time; because of this the populations are even more likely to face extinction *sensu* Kuussaari *et al*. (2009).

Compounding Factors

In the central part of its range, where yew creates dense, pure woodlands, some regeneration appears in gaps with shrubs but mostly it occurs in light, open areas surrounding existing woodlands (Svenning & Magård, 1999 Thomas & Polwart, 2003; Devaney *et al*., 2014). This is likely to expose seeds (which mostly germinate in the second or even third year after reaching the ground – Melzack & Watts, 1982) and new seedlings to the full force of the changing climate. In the south, where yew is scattered through more open woodlands, this may cause less of a problem since the seedlings will have some overstorey above them buffering them from harsh conditions and the yew seedlings will still be highly competitive (Iszkuło & Boratyński, 2006; Dhar *et al*., 2007; Ruprecht *et al*., 2010).

A further complication is that the competitive species will change with climate. For example in Lithuania, the current climate is suitable for yew but populations are small. But by 2031-2060, Ozolinčius *et al*. (2014) suggest that the climate will be suitable for a number of highly competitive species including sycamore *Acer pseudoplatanus*, beech *Fagus sylvatica*, and to a lesser extent field maple *Acer campestre*, which will invade the forests. By 2061–2090 these will be joined by large leaved lime *Tilia platyphyllos*, with the potential to change the success of yew regeneration (Packham *et al*., 2012). At the end of the twenty-first century, sweet chestnut *Castanea sativa* could also invade the woodland, further increasing competition against the yew, itself weakened by climate change.

Seed production of yew is likely to decrease with climate change. Implicit in this is reduced pollen production with increasing temperatures. Mercuri *et al*. (2013) noted that in northern Italy the amount of pollen being produced by yew declined over an 18 year period while at the same time the overall pollen concentration of total woody species went up. Yew acts as a winter flowering plant and so, paradoxically, pollen production is delayed in spring with warmer temperatures and stops sooner, producing a shorter pollen release period. Being dioecious, with separate male and female trees, pollination is more successful with male and female trees in close proximity. Long-term population fragmentation and shrinking population size are thus likely to lead to lower fertilization and production of viable seed (Fahrig, 2002, 2003; Allison, 1990). This is being compounded by a decrease in the proportion of females in response to climate. Iszkuło *et al*. (2009) found that drought leads to loss of female trees in competition with males. Their findings agree with previous research (Obeso, 2002) that the increased reproductive effort in females appears to make them more susceptible to the effects of drought. Certainly, while growth is negatively correlated with high temperatures in August and September, females in western Poland produce wider rings in wetter summers (Cedro & Iszkuło, 2011).

It is also highly likely that population changes in animal seed-dispersers associated with yew will affect yew regeneration. Removal of larger mammals and birds is highly likely to reduce the long-distance dispersal of seeds (the Empty Forest Syndrome of Jordano *et al*., 2007) with consequent reduction in genetic mixing. Loss of the larger fauna may also have a direct effect on seed size, with smaller birds taking only smaller seeds, potentially leading to a rapid evolutionary reduction in seed mass as has been seen in other species (Galetti *et al*., 2013) which would reduce the probability of regeneration success since smaller seed and thus seedlings would be more prone to drought stress.

Smaller and more isolated populations also produce a high degree of inbreeding in yew populations (Dubreuil *et al*., 2008; Myking *et al*., 2009) limiting the genetic diversity. Indeed, Lewandowski *et al*. (1995) noted that new progeny show much higher levels of inbreeding, probably because of limited seed-dispersal and mating between close neighbours. However, they also showed that loss of genetic variation in depleted populations is not necessarily a problem since a strongly declining population in Poland showed high levels of genetic diversity. This is probably because yew is an inherently genetically variable species compared with other conifers (Ledig, 1986) and high genetic variation is encouraged by dioecy and wind pollination.

Conclusions

It is clear from the above that while yew trees will survive in the short-term, and may even expand in number, the adult trees will gradually succumb to environmental pressure albeit slowly within the main range but especially in southern Europe. Long before that, regeneration will have largely disappeared particularly in the south and certainly decreased in the centre and north of its current range. This will happen without the benefit of the range expanding to the north and providing new territory with a cooler, wetter climate. Without human intervention, in the long-term yew will go into an ‘extinction debt’ in many areas, that is, it will effectively be an extinct species with no reproduction but the last individuals have yet to die. Indeed many southern populations are likely to already be at this stage. For many of us this would be a disaster in itself, but it also has wider implications than the loss of one species since yew is home to myriad insects and fungi (Thomas & Polwart, 2003) and other ecosystem services including carbon storage; loss of old trees in old woodlands will lower primary productivity and carbon storage (Bonan 2008, Michaletz *et al*., 2014).

Conservation programmes are already underway throughout the range of yew (e.g. Dhar *et al*., 2007; Piovesan *et al*., 2009) but where should the priorities lie? The exact order of priority will, of course vary depending upon geographical location and dominant environmental stressors, and upon local management objectives, but we offer the following recommendations in approximate order of effectiveness weighed against cost.

- In forests that contain yews such as old-growth beech forests, but also young aggressively-growing beech stands or monoculture plantations (Schwendtner, 2011; Iszkulo *et al*., 2012), a degree of selective thinning to reduce timber volume by around 10-20% provides beneficial light to yew trees without unduly stimulating competitive species (Dahr *et al*., 2006: Ruprecht *et al*., 2010). Long-term rotations, with lengthy periods between extensive felling operations, and preferably continuous cover forestry rather than clear felling would also be beneficial (Dhar *et al*., 2007; Farris & Filigheddu, 2008).
- Habitat improvement by maintaining a multi-layered canopy structure to provide a dense, protective habitat to maintain a suitable microclimate (e.g. oceanic in the south; protection from frost in the north), especially in those in climatically marginal conditions. This should be allied to reduced felling of woody plants surrounding the yews in these marginal conditions (but see above).
- In southern and eastern areas, protecting yew stands from fire with the judicious use of fire breaks and fuel reduction particularly downslope of vulnerable stands.
- Planting and maintaining seedlings through their vulnerable first years giving protection where necessary from grazing and high winds which can desiccate in summer and allow frost damage in the north in winter. Ideally, yew populations should have an area of at least 0.5–3.0 ha to be self-perpetuating (Piovesan *et al*., 2009) together with a minimum number of 40 individuals with more or less equal proportions of males and females (Iszkuło *et al*., 2009). Irrigation of seedlings in dry seasons is also crucial to their survival.
- The improvement and restoration of *Taxus* habitat by providing microhabitats for pollinators and seed dispersers, such as by creating drinking points and planting fleshy-fruited plants, creating heterogeneous spaces with high density of these plants to attract dispersers (Garcia-Martí & Ferrer, 2013).
- Creating live ex-situ and quasi in-situ collections in safe environments away from possible disturbance. These can operate as seed orchards to ensure a supply of seed that can be used to supplement yew populations where the number of reproductive individuals or overall seed production is too low to be viable under increasing climatic restrictions.
- Relieving the stress on adult and old veteran trees and protecting established reproductive individuals. For isolated individuals in the open, and to a lesser extent in dense yew woodlands, this might require irrigation to reduce the effects of high summer temperatures/high evapotranspiration, and possibly artificial shade in the short-term, and growing tall nearby trees to provide the same in the long-term.
- Safeguarding and enhancing the genetic diversity of small and endangered populations across dif-

ferent spatial scales. Safeguarding diversity is most readily achieved by maintaining as many individuals as possible in each population. Genetic enhancement is possible by moving seed or seedlings from one area to another but this should be underpinned by research to ensure that new individuals would be contributing new genes. Which new genes would be particularly beneficial to a populations is still largely unknown but management should pragmatically be based on the assumption that greater genetic diversity will be beneficial and not detrimental.

- Promoting the connectivity at both inter- and intra-population levels to improve the resilience of remnant populations (Krosby *et al*., 2010).
- Movement of seeds from southern provenances to places further north. This requires decisions on what sort of future climate is being planned for, and using this as a basis for deciding from where the seeds should be brought. The warmer the conditions planned for, the further south the donor site. At the southern end of the range this obviously presents problems since no more southerly seed are available. Moreover, there is no guarantee that southern seed will perform well further north due to other ecological factors such as lack of resistance to pathogens, changes in phenology, etc. (Thomas, 2014). To our knowledge there have been no provenance trials of yew. However, given the high inherent genetic diversity of yew populations (Lewandowski *et al*., 1995), the best solution is likely to be to plant a greater number of local provenance seeds with the expectation that at least some will be pre-adapted for coping with warmer, drier conditions.

The main objective of any management must be to safeguard older trees (both as seed sources but also because the oldest trees are irreplaceable in the lifetime of humans), ensure regeneration of the next trees, and maintain the ecological integrity of stands that contain yews. In this way species dependant on yew will continue to thrive, and many generations to come will enjoy this splendid tree.

Acknowledgements

Our thanks to the people who have contributed so much to the literature on the ecology of yews and to the many people with whom we had discussions, arguments and agreements on a wide range of yew and climate change issues. This review is based on papers presented by the authors at the IV International Yew Workshop, Poblet, Spain, kindly organised and funded by the CTFC (Forest Sciences Centre of Catalonia), Solsona, Spain.

References

AEMET - Agencia Estatal de Meteorología, 2014. http://www.aemet.es/es/noticias/2014/10/hidrologico2013-2014. [5 January 2015].

Alcober JA, Sanchís E, Crespo MB, 1988. Distribución y autoecología del tejo (*Taxus baccata* L.) en la provincia de Valencia. Ecología 2: 131-138.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH et al., 2009. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecol Manage 259: 660-684. http://dx.doi.org/10.1016/j.foreco.2009.09.001.

Allison TD, 1990. Pollen production and plant density affect pollination and seed production in *Taxus canadiensis.* Ecology 71: 516-522. http://dx.doi.org/10.2307/1940305.

Bonan, GB, 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320: 1444-1449. http://dx.doi.org/10.1126/science.1155121.

Brzeziecki B, Kienast F, 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. Forest Ecol Manag 69: 167-187. http://dx.doi.org/10.1016/0378-1127(94)90227-5.

Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM, 2105. To die or not to die: early warnings of tree dieback in response to a severe drought. J Ecol 103: 44-57. http://dx.doi.org/10.1111/1365-2745.12295.

Carvalho A, Rebelo A, Dias J, 1999. Distribution and natural regeneration of yew trees in the National Parks of Peneda-Geres (Portugal) and Baixa Limia Serra-Xures (Spain). Rev Biol 17: 43-49.

Caughley G, 1994. Directions in conservation biology. J Anim Ecol 63: 215-244.http://dx.doi.org/10.2307/5542.

Cedro A, Iszkuło G, 2011 Do females differ from males of European yew (*Taxus baccata* L.) in dendrochronological analysis? Tree-Ring Res 67: 3-11.http://dx.doi.org/10.3959/2009-9.1.

Charco J, 2007. El tejo en el norte de África. In: El tejo en el Mediterráneo Occidental (Serra L, ed). Conselleria de Territori i Habitatge. Ministerio de Medio Ambiente de España. CAM. pp: 177-185.

Cortés S, Vasco F, Blanco E, 2000. El libro del tejo. Ed. Arba. Madrid, España.

Costa JC, 2007. Distribución y ecología de las tejedas en Andalucía: Propuesta de ctuaciones de conservación, regeneración y restauración. In: El tejo en el Mediterráneo Occidental (Serra L, ed). Conselleria de Territori i Habitatge. Ministerio de Medio Ambiente de España. CAM. pp:161-171.

Devaney JL, Jansen MAK, Whelan PM, 2014 Spatial patterns of natural regeneration in stands of English yew (*Taxus* *baccata* L.); Negative neighbourhood effects. Forest Ecol Manag 321: 52-60. http://dx.doi.org/10.1016/j.foreco.2013.06.060.

Dhar A, Ruprecht H, Klumpp R, Vacik H, 2006. Stand structure and natural regeneration of English yew (*Taxus baccata* L.) at Stiwollgraben in Austria. Dendrobiology 56: 19-26.

Dhar A, Ruprecht H, Klumpp R, Vacik H, 2007. Comparison of ecological condition and conservation status of English yew population in two Austrian gene conservation forests. J Forest Res 18: 181-186. http://dx.doi.org/10.1007/s11676-007-0037-5.

Dubreuil M, Sebastiani F, Mayol M, González-Martínez SC, Riba M, Vendramin GG, 2008. Isolation and characterization of polymorphic nuclear microsatellite loci in *Taxus baccata* L. Conserv Genet 9:1665-1668. http://dx.doi.org/10.1007/s10592-008-9515-3.

Elwes HJ, Henry A, 1906. The Trees of Great Britain and Ireland. Privately printed, Edinburgh, UK. http://dx.doi.org/10.5962/bhl.title.53977.

European Commission, 2007. Interpretation manual of European Union Habitats – EUR27. DG Environment, European Commission.

Fahrig L, 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecol Appl 12: 346–353.

Fahrig L, 2003. Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34: 487–515. http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132419.

Farris E, Filigheddu R, 2008. Effects of browsing in relation to vegetation cover on common yew (*Taxus baccata* L.) recruitment in Mediterranean environments. Plant Ecol 199: 309-318. http://dx.doi.org/10.1007/s11258-008-9434-x.

Fernández-Manso O, Fernández-Manso A, Santamaría E, Quintano C, 2011. Análisis territorial de la Tejedas de Castilla y León (España). SJRD 2: 69-80.

Galetti M, Guevara R, Côrtes MC, Fadini R, Von Matter S, Leite AB, Labecca F, Ribeiro T, Carvalho CS, Collevatti RG, et al., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340: 1086-1090.http://dx.doi.org/10.1126/science.1233774.

García-Martí X, Ferrer P, 2013. La creación de núcleos de dispersión – reclamo como modelo de restauración ecológica forestal. In: Avances en la restauración de sistemas forestales. Técnicas de implantación (Martínez-Ruiz C, Lario FJ, Fernández-Santos B, eds.) SECF-AEET, Madrid, España. pp: 149-159.

García D, Obeso JR, 2003. Facilitation by herbivore-mediated nurse plants in a threatened tree, *Taxus baccata*: local effects and landscape level consistency. Ecography 26: 739-750. http://dx.doi.org/10.1111/j.0906-7590.2003.03601.x.

García D, Zamora R, Hódar JA, Gómez JM, Castro J, 2000. Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. Biol Cons 95: 31-38. http://dx.doi.org/10.1016/S0006-3207(00)00016-1.

Grubb PJ, 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52: 107-145. http://dx.doi.org/10.1111/j.1469-185X.1977.tb01347.x.

Hageneder F, 2007. Yew a history. Sutton Publishing, Stroud, Gloucestershire, UK.

Hamidouche-Si MC, Bouahmed A, Vesella F, Krouchi F, Arezki D, 2014. Geographic distribution and morphological variation of *Taxus baccata* in Algeria. Der Eibenfr 20: 39-53.

Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann KE, 2013. Climate change may cause severe loss in the economic value of European forest land. Nat Clim Change 3: 203-207. http://dx.doi.org/10.1038/nclimate1687.

Harper JL, 1977. Population biology of plants. Academic Press, London, UK.

Hättenschwiler S, 2001. Tree seedling growth in natural deep shade: functional traits related to interspecific variation in response to elevated CO_2. Oecologia 129: 31-42. http://dx.doi.org/10.1007/s004420100699.

Hättenschwiler S, Körner C, 2000. Tree seedling responses to in situ CO_2-enrichment differ among species and depend on understorey light availability. Glob Change Biol 6: 213-226. http://dx.doi.org/10.1046/j.1365-2486.2000.00301.x.

IPCC, 2013. Climate change 2013. The physical science basis. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.

Iszkuło G, 2010. Success and failure of endangered tree species: low temperatures and low light availability affect survival and growth of European yew (*Taxus baccata* L.) seedlings. Pol J Ecol 58: 259-271.

Iszkuło G, Boratyński A, 2006. Analysis of the relationship between photosynthetic photon flux density and natural *Taxus baccata* seedlings occurrence. Acta Oecol 29: 78-84. http://dx.doi.org/10.1016/j.actao.2005.08.001.

Iszkuło G, Didukh Y, Giertych MJ, Jasińska AK, Sobierajska K, Szmyt J, 2012. Weak competitive ability may explain decline of *Taxus baccata*. Ann For Sci 69: 705-712. http://dx.doi.org/10.1007/s13595-012-0193-4.

Iszkuło G, Jasińska AK, Giertych MJ, Boratyński A, 2009. Do secondary sexual dimorphism and female intolerance to drought influence the sex ratio and extinction risk of *Taxus baccata*? Plant Ecol 200: 229-240. http://dx.doi.org/10.1007/s11258-008-9447-5.

Jordano P, García C, Godoy JA, García-Castaño JL, 2007. Differential contribution of frugivores to complex seed dispersal patterns. PNAS 104: 3278-3282. http://dx.doi.org/10.1073/pnas.0606793104.

Kassioumis K, Papageorgiou K, Glezakos T, Vogiatzakis IN, 2004. Distribution and stand structure of *Taxus baccata* populations in Greece; Results of the first national inventory. Ecologia Medit 30: 159-170.

Katsavou I, Ganatsas P, 2012. Ecology and conservation status of *Taxus baccata* population in NE Chalkidiki, northern Greece. Dendrobiology, 68: 55-62.

Krosby M, Tewksbury J, Haddad NM, Hoekstra J, 2010. Ecological connectivity for a changing climate. Conserv Biol 24: 1686-1689. http://dx.doi.org/10.1111/j.1523-1739.2010.01585.x

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Roda F, et al., 2009. Extinction debt: a challenge for biodiversity conservation. Trends Ecol Evol 24: 564-571. http://dx.doi.org/10.1016/j.tree.2009.04.011.

Lange OL, 1961. Die Hitzeresistenz einheimischer immerund wintergrüner Pflanzen im Jahreslauf. Planta 56: 666-683. http://dx.doi.org/10.1007/BF01928210.

Ledig FT, 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. In: conservation biology: the science of scarcity and diversity (Soule ME, ed). Sinauer, Sunderland, Massachusetts, USA. pp: 77-104.

Lewandowski A, Burczyk J, Mejnartowicz L, 1995. Genetic structure of English yew (*Taxus baccata* L.) in the Wierzchlas Reserve: implications for genetic conservation. Forest Ecol Manag 73: 221-227. http://dx.doi.org/10.1016/0378-1127(94)03477-E.

Linares JC, 2013. Shifting limiting factors for population dynamics and conservation status of the endangered English yew (*Taxus baccata* L., Taxaceae). Forest Ecol Manag 291: 119-127. http://dx.doi.org/10.1016/j.foreco.2012.11.009.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD, 2009. The velocity of climate change. Nature 462: 1052-1055. http://dx.doi.org/10.1038/nature08649.

Martínez I, Taboada FG, Wiegand T, Obeso JM, 2013. Spatial patterns of seedling-adult associations in a temperate forest community. Forest Ecol Manag 296: 74-80. http://dx.doi.org/10.1016/j.foreco.2013.02.005.

Melzack RN, Watts D, 1982. Variations in seed weight, germination, and seedling vigour in the yew (*Taxus baccata* L.) in England. J Biogeogr 9: 55-63. http://dx.doi.org/10.2307/2844730.

Mendoza I, Gómez-Aparicio L, Zamora R, Matías L, 2009a. Recruitment limitation of forest communities in a degraded Mediterranean landscape. J Veg Sci 20: 367-376. http://dx.doi.org/10.1111/j.1654-1103.2009.05705.x.

Mendoza I, Zamora R, Castro J, 2009b. A seeding experiment for testing tree community recruitment under variable environments: implications for forest regeneration and conservation in Mediterranean habitats. Biol Conserv 142: 1491-1499. http://dx.doi.org/10.1016/j.biocon.2009.02.018.

Mercuri AM, Torri P, Casini E, Olmi L, 2013. Climate warming and the decline of *Taxus* airborne pollen in urban pollen rain (Emilia Romagna, northern Italy). Plant Biol 15 (Suppl. 1): 70-82. http://dx.doi.org/10.1111/j.1438-8677.2012.00624.x.

Michaletz ST, Cheng D, Kerkhoff AJ, Enquist BJ, 2014. Convergence of terrestrial plant production across global climate gradients. Nature 512: 39-43. http://dx.doi.org/10.1038/nature13470.

Myking T, Vakkari P, Skrøppa T, 2009. Genetic variation in northern marginal *Taxus baccata* L. populations. Implications for conservation. Forestry 82: 529-539. http://dx.doi.org/10.1093/forestry/cpp022.

Obeso JR, 2002. The costs of reproduction in plants. New Phytol 155: 321-348. http://dx.doi.org/10.1046/j.1469-8137.2002.00477.x.

Ozolinčius R, Lekevičius E, Stakėnas V, Galvonaitė A, Samas A, Valiukas D, 2014. Lithuanian forests and climate change: possible effects on tree species composition. Eur J For Res 133: 51-60. http://dx.doi.org/10.1007/s10342-013-0735-9.

Packham JR, Thomas PA, Atkinson MD, Degen T, 2012. Biological flora of the British Isles. *Fagus sylvatica* L. J Ecol 100: 1557-1608. http://dx.doi.org/10.1111/j.1365-2745.2012.02017.x.

Pausas JG, 2004. Changes in fire and climate in the eastern Iberian Peninsula. Clim Change 63: 337-350. http://dx.doi.org/10.1023/B:CLIM.0000018508.94901.9c.

Pearson RG, Dawson TP, 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecol Biogeogr 12: 361-371. http://dx.doi.org/10.1046/j.1466-822X.2003.00042.x.

Pearson RG, Dawson TP, Berry PM, Harrison PA, 2002. SPECIES: a spatial evaluation of climate impact on the envelope of species. Ecol Model 154: 289-300. http://dx.doi.org/10.1016/S0304-3800(02)00056-X.

Peñuelas J, Filella I, Piñol J, Siscart D, Lloret, F, 2000. Effects of a severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*. Biol Plantarum 43: 47-53. http://dx.doi.org/10.1023/A:1026546828466.

Peñuelas J, Ogaya R, Boada M, Jump AS, 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain) Ecography 30: 829-837. http://dx.doi.org/10.1111/j.2007.0906-7590.05247.x.

Piñol J, Terradas J, Lloret F, 1998. Climate warming, wildfire hazard and wildfire occurrence in coastal Eastern Spain. Clim Change 38: 345-357. http://dx.doi.org/10.1023/A:1005316632105.

Piovesan G, Presutti Saba E, Biondi F, Alessandrini A, Di Filippo A, Schirone B, 2009. Population ecology of yew (*Taxus baccata* L.) in the Central Apennines: spatial patterns and their relevance for conservation strategies. Plant Ecol 205: 23-46. http://dx.doi.org/10.1007/s11258-009-9596-1.

Pisek A, Larcher W, Moser W, Pack I, 1969. Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. III. Temperaturabhangigkeit und optimaler Temperaturbereich der Netto-Photosynthese. Flora 158: 608-630.

Preston CD, Pearman DA, Dines TD 2002. New atlas of the British and Irish flora. Oxford University Press, Oxford, UK.

Rodwell JS, 1991. British plant communities. Vol. 1 Woodlands and scrub. Cambridge University Press, Cambridge, UK.

Ruprecht H, Dhar A, Aigner B, Oitzinger G, Klumpp R, Vacik H, 2010. Structural diversity of English yew (*Taxus baccata* L.) populations. Eur J For Res 129: 189-198. http://dx.doi.org/10.1007/s10342-009-0312-4.

Sanz R, Pulido F, Nogués-Bravo D, 2009. Predicting mechanisms across scales: amplified effects of abiotic constraints on the recruitment of yew *Taxus baccata*. Ecography 32: 993-1000. http://dx.doi.org/10.1111/j.1600-0587.2009.05627.x.

Saura S, Martín-Queller E, Hunter ML, 2014. Forest landscape change and biodiversity conservation. In: Forest landscapes and global change: challenges for research and management (Azevedo JC, Perera AH, Pinto MA, eds). Springer, Berlin (Germany). pp: 167-198. http://dx.doi.org/10.1007/978-1-4939-0953-7_7.

Schwendtner O, 2011. Supervivencia y crisis del tejo (*Taxus baccata* L) en el área cantábrica. In: II Jornadas del Tejo en el Mediterráneo Occidental (Caritat A, ed). Delegació en la Garrotxa de la Institució Catalana de Historia Natural i Fundació Estudis Superiors d'Olot (Girona, Spain). pp: 43-49.

Seidling W, 1999. Spatial structures of a subspontaneous population of *Taxus baccata* saplings. Flora 194: 439-451.

Serra L, Garcia-Martí X, 2011. Distribución del tejo en España. In: II Jornadas del Tejo en el Mediterráneo Occidental (Caritat A, ed). Delegació en la Garrotxa de la Institució Catalana de Historia Natural i Fundació Estudis Superiors d'Olot (Girona, Spain). pp:17-43.

Svenning J-C, Magård E, 1999. Population ecology and conservation status of the last natural population of English yew *Taxus baccata* in Denmark. Biol Conserv 88: 173-182. http://dx.doi.org/10.1016/S0006-3207(98)00106-2.

Svenning J-C, Skov F, 2004. Limited filling of the potential range in European tree species. Ecol Lett 7: 565-573. http://dx.doi.org/10.1111/j.1461-0248.2004.00614.x.

Sykes MT, Prentice IC, Cramer W, 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. J Biogeogr 23: 203-233.

Thomas PA, 2014. Trees: their natural history (2nd ed). Cambridge University Press, Cambridge, UK.

Thomas PA, Polwart A, 2003. Biological flora of the British Isles. *Taxus baccata* L. J Ecol 91: 489-524. http://dx.doi.org/10.1046/j.1365-2745.2003.00783.x.

Till O, 1956. Über die Frosthärte von Pflanzen sommergrüner Laubwälder. Flora 143: 499-542.

Tittensor RM, 1980. Ecological history of yew *Taxus baccata* L. in southern England. Biol Conserv 17: 243-265. http://dx.doi.org/10.1016/0006-3207(80)90026-9.

Voliotis D, 1986. Historical and environmental significance of the yew (*Taxus baccata* L.). Israel J Bot 35, 47-52.

Watt AS, 1926. Yew communities of the South Downs. J Ecol 14: 282-316. http://dx.doi.org/10.2307/2256022.

Williamson R, 1978. The great yew forest – the natural history of Kingley Vale. Macmillan, London, UK.

Zhu K, Woodall CW, Clark JS, 2012. Failure to migrate: lack of tree range expansion in response to climate change. Glob Change Biol 18: 1042-1052. http://dx.doi.org/10.1111/j.1365-2486.2011.02571.x.